Age, Growth, and Size Distribution of Larval Atlantic Menhaden off North Carolina

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Abstract.—Counts of growth increments on sagittal otoliths of larval Atlantic menhaden Brevoortia tyrannus spawned and reared in the laboratory showed that 1 increment/d was formed beginning 5 d after fertilization and that increment counts could be used to estimate larval age. A Gompertz growth equation described the relationship between age and standard length (SL) for 353 larvae collected off North Carolina in fall and winter, 1979–1980. Larvae grew from 3.4 mm SL at hatching to 25.2 mm SL at 100 d. Age of larvae varied inversely with capture distance from shore. Age distribution of larvae on the North Carolina continental shelf suggests that transport of larvae from offshore spawning sites to the estuary was biphasic. Transport was relatively rapid to within about 35 km of shore and relatively slow from there to shore. Mean age at estuarine recruitment increased from 40 to 80 d throughout the recruitment season, which may represent differences in transport rate.

Conspicuously absent from life history summaries of Atlantic menhaden Brevoortia tyrannus are references on the age and growth of the species' early life stages (Reintjes 1969; Ahrenholz et al. 1987; Lewis et al. 1987). June and Roithmayr (1960) established the validity of using scales to age adult Atlantic menhaden, and Simoneaux and Warlen (1987) showed that sagittal otoliths can be used to age juveniles. However, only recently has otolith microstructure been used to age Atlantic menhaden larvae (Maillet and Checkley 1990). The technique has also been validated for larvae of gulf menhaden B. patronus by Warlen (1988), who measured their age and growth in the northern Gulf of Mexico. Larval growth rates of Atlantic menhaden have been measured in the laboratory from hatching to 21 d (Powell and Phonlor 1986) and to 36 d (Maillet and Checkley 1990), but there are no studies on the growth of Atlantic menhaden larvae in the wild.

The objectives of this study were (1) to evaluate the frequency with which sagittal otolith growth increments are deposited in larval Atlantic menhaden, (2) to estimate the growth of larvae from the time they are spawned offshore on the continental shelf to the time they enter estuaries as advanced larvae, and (3) to examine the age and size distributions of larvae along a transect perpendicular to the North Carolina coast from Beaufort Inlet to the Gulf Stream.

Methods

Spawning and rearing of larvae. - Adult Atlantic menhaden were collected near Beaufort, North

Carolina in late summer 1986. After a period of acclimation, adults were induced to spawn in the laboratory by the methods of Hettler (1981). Larvae were used in experiments to validate the periodicity of increment formation on their sagittal otoliths and the age at first increment formation.

Experiments began in February 1987, when several thousand newly spawned Atlantic menhaden eggs were transferred to a tank containing 90 L of filtered seawater. Static water in the tank was aerated continuously and kept at a temperature of 20.5 \pm 0.5°C and a salinity of 33 \pm 1‰. Photoperiod was 12 h light: 12 h dark. Beginning 3 d after hatching, larvae were fed ad libitum with the rotifer Brachionus plicatilis. Rotifers were supplemented three times weekly with wild plankton small enough to pass through a 202-µm-mesh filter. A green alga, Nanochloris sp., was added weekly as food for the rotifers and to aid in removing toxic metabolites. The bottom of the tank was cleaned three times weekly and dead or dying fish were removed. Laboratory-reared larvae were sampled 18, 25, 32, and 41 d postfertilization and preserved with 95% ethanol.

Larval collections.—Monthly sampling for larvae was conducted off Beaufort, North Carolina, during five 2-d cruises on the R/V John deWolf II from November 1979 through March 1980. On each cruise, stations were sampled along a transect from Beaufort Inlet to about the 183-m contour (Figure 1). At all stations except Beaufort Inlet, where only a surface tow was made, samples were obtained with oblique hauls (Powles and Stender 1976) of 60-cm-diameter bongo nets (mesh sizes,

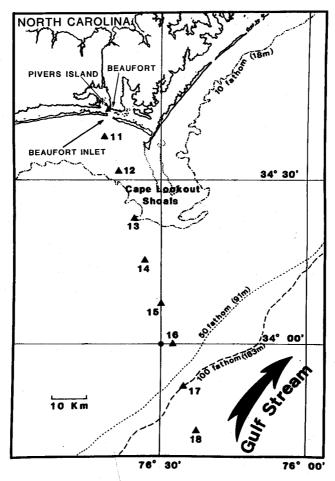


FIGURE 1.—Locations of sampling sites for larval Atlantic menhaden in the mouth of the Newport River estuary at Pivers Island and in the ocean off Beaufort Inlet, North Carolina.

333 and 505 μ m) rigged with flow meters. Larvae were also collected with a neuston net (Hettler 1979) about 2 km inside Beaufort Inlet at Pivers Island (Figure 1) on several dates. All samples were preserved with 95% ethanol within 5 min of collection.

Age and growth estimation.—The standard length (SL) of each larva was measured to the nearest 0.1 mm with an ocular micrometer. Sagittal otoliths were teased from the surrounding tissue, cleaned in distilled water, and then placed on a glass microscope slide under a thin layer of Flo-Texx¹ mounting medium.

Otoliths were viewed with transmitted light

through a compound microscope fitted with a television camera. Growth increments were counted from images on a video monitor at microscope magnifications of 400× or 1,000×. Each increment appeared as a light, wide band with an adjoining dark, narrow, discontinuous band (Tanaka et al. 1981). In most cases, increments were clearly discernable and easily counted, and they resembled those described for gulf menhaden larvae (Warlen 1988). Increments on otoliths of laboratory-reared fish were counted by the same reader on two separate occasions. The mean increment count was compared to the known age. After expertise was developed in discerning growth increments in laboratory-reared fish, growth increments on otoliths of wild-caught larvae were counted one time for each fish. Estimated age of a larva was the number of increments counted

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

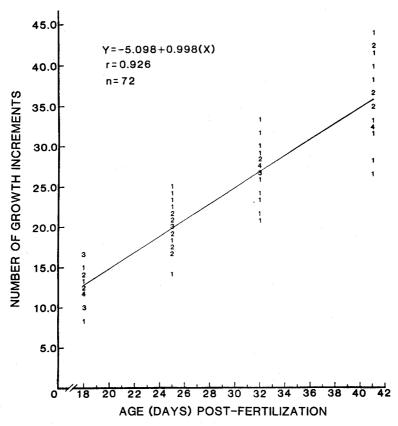


FIGURE 2.—Regression of the number of growth increments (Y) on the known postfertilization age (X) of 72 laboratory-reared Atlantic menhaden larvae (numbers along regression). Standard error of the slope is 0.048.

plus an empirically derived value for the number of days from spawning to first increment formation.

Average growth of wild-caught larvae was described by the Laird version (Laird et al. 1965) of the Gompertz growth equation (Zweifel and Las-

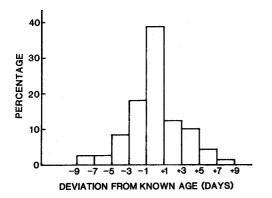


FIGURE 3.—Accuracy of estimating age of 72 laboratory-reared Atlantic menhaden larvae of known age.

ker 1976). The model was fitted to data for size and estimated age at time of capture. To stabilize the variance of length over the observed age interval, length data were log-transformed and model parameters were estimated from the log-transformed version of the growth equation (Warlen 1988).

Results

Growth Increment Formation

The age of Atlantic menhaden at formation of the first growth increment was estimated from laboratory-reared larvae. The regression of the number of growth increments on known postfertilization age of 72 larvae (Figure 2) was significant $(F=427.39,\,\mathrm{df}=1,\,70,\,P<0.01)$. The intercept of the equation (rounded to 5.0 d) was used to estimate time from spawning to first increment formation. This value was added to the increment count to estimate the age of larvae from spawning. The slope (0.998) of the regression was not significantly different from 1.0 (t-test, P>0.01); thus,

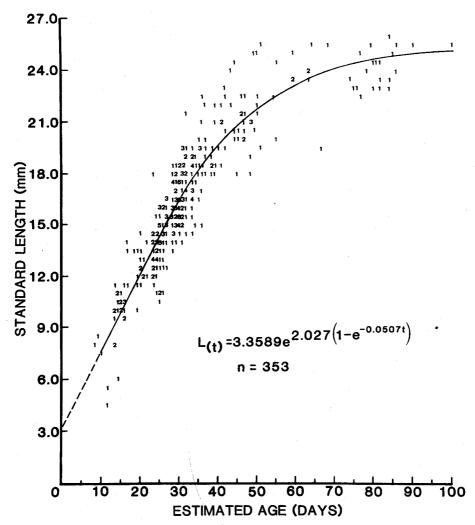


FIGURE 4.—Growth of 353 Atlantic menhaden larvae (numbers along curve) collected from oceanic and estuarine waters of North Carolina during the period November 1979–April 1980. The Laird–Gompertz growth model was used to describe the data; L is standard length and t is age.

on the average, one otolith growth increment was formed per day in larval Atlantic menhaden reared for 41 d after fertilization. For subsequent analyses, I assumed that the growth increment deposition rate in wild-caught larvae was also one per day. Growth increments in wild-caught larvae were more easily read than those in laboratory-reared larvae.

The precision in duplicate otolith readings for laboratory-reared larvae was estimated from the differences in the paired readings of the data from Figure 2. The mean (\pm SD) differences in readings were 1.2 \pm 1.0 d, 2.0 \pm 2.2 d, 2.2 \pm 2.0 d, and 3.7 \pm 2.9 d for fish of known ages 18, 25, 32, and 41 d. Accuracy of estimating the ages of those 72

known-age larvae was assessed from a frequency distribution of the deviation of the estimated age from the known age for each fish. A summary of these data (Figure 3) indicated that about 70% of the laboratory-reared larvae were aged to within ± 3 d and that overaging and underaging errors were similar.

Larval Growth

The average growth of larval Atlantic menhaden collected in the ocean and at Pivers Island during their first 3 months was described by the Gompertz model fitted to the age and standard length data for 353 larvae (Figure 4). Larvae ranged in age from 8 to 100 d (mean, 33.6 d) and in SL

TABLE 1.—Estimated average growth (mm/d) of field-caught larval Atlantic menhaden for 20-d intervals from hatching to 100 d. The estimated size at day 1 (3.36 mm standard length) and sizes at other points were estimated from the growth model in Figure 4.

Interval (d)	Average growth during interval (mm/d)	
1–20	0.47	
21-40	0.36	
41–60	0.18	
61-80	0.07	
81-100	0.03	

from 4.7 to 25.9 mm (mean, 16.1 mm). In the log-transformed model, age accounted for 83% of the variation in length. From the predicted size at hatching of 3.4 mm, larvae grew to 25.2 mm SL by 100 d. Average daily growth rate declined from 0.47 mm/d during the age interval of 1–20 d to 0.03 mm/d during the age interval of 81–100 d (Table 1), and the overall average rate was 0.22 mm/d. Age-specific growth rate declined from about 6%/d at 10 d to less than 0.11%/d at 90 d.

Larval Transport

The relationship between age or SL and capture distance from Beaufort Inlet was approximated (Figure 5) for only three cruises (January, February, March), because there were insufficient data from the other two cruises. Frequency distributions of the ages of larvae (Figure 6) suggested that larval age varied inversely with distance from shore, and the trend was similar for all three cruises. Youngest larvae were usually found farthest offshore (out to 110 km) and ages of larvae increased relatively little shoreward to about 35 km offshore (Figure 5). A linear regression (t-test, P < 0.01) of the ages of fish at stations 14–18 versus distance from Beaufort Inlet (Figure 7) indicated relatively rapid transport at least halfway across the continental shelf. The difference in the predicted ages of larvae (from the regression) at stations 14 and 18 divided by the distance (58 km) between those stations was used to calculate a general larval transport rate of 4.4 km/d. The absence of a significant difference between the intercept of the regression (40.9 d) and the mean age of larvae caught at the Inlet in December or April (Table 2) suggests that larval transport rates sometimes were similar both inshore and offshore of station 14. However, significant differences between the intercept and the mean age of larvae collected in January, February, and March (Table 2) suggest

reduced transport rates inshore of station 14 during winter. Transport rates for those months (2.3, 1.5, and 1.0 km/d) were estimated by dividing the offshore distance of station 14 (51 km) by the respective differences in mean age at estuarine recruitment and the predicted age of larvae (29.3 d) at station 14. The mean age of larvae collected near Beaufort Inlet increased from 41 d in early December to 79 d in mid-March (Table 2). By April the mean estimated age of larvae had decreased to levels observed in early December 1979.

Mean standard length also varied inversely with capture distance from shore (Figure 5). Larvae collected farthest offshore (station 18) averaged 9.7 or 12.4 mm SL. Mean larval size at Beaufort Inlet ranged from 20.7 to 26.5 mm SL (Table 2; Figure 5).

Discussion

The laboratory experiments indicated that the age of larval Atlantic menhaden can be estimated from counts of their otolith growth increments. Initial deposition of countable increments coincided with the time of first exogenous feeding, which usually occurs about 4 d posthatch at 18°C (Powell and Phonlor 1986) or about 5 d after spawning; increment deposition continued daily thereafter. Maillet and Checkley (1990) also found that Atlantic menhaden larvae deposited daily growth increments, but that larvae initiated increment formation at hatching. However, the 3-4 posthatch increments that they observed before larvae began feeding were narrow ($<1 \mu m$), poorly defined, and not consistently resolvable with light microscopy. They concluded that the first prominent growth increment was formed at first feeding. Their validation results and those of this study are complementary. In both studies, sagittal otolith growth increments were counted beginning with the first prominent one. However, it is necessary to add an estimate of the number of days from spawning to first feeding (i.e., 5 d, the rounded intercept of the age-increment regression: Figure 2) to the increment count in order to estimate the total postfertilization age of a wild larva. The time from spawning to first feeding is temperature dependent (Powell and Phonlor 1986), and because the thermal environmental history of wild larvae is unknown, estimated times from spawning to first feeding vary. For example, the difference in age at first feeding at 17°C and 20°C was 1.3 d (estimated from Figure 3 of Powell and Phonlor 1986).

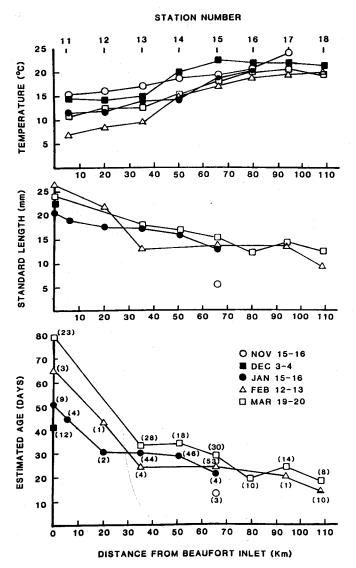


FIGURE 5.—Surface water temperature, mean standard length, and mean estimated age of Atlantic menhaden larvae collected during the period November 1979—March 1980 along the transect shown in Figure 1. Numbers in parentheses represent the number of fish in the sample.

The Laird-Gompertz growth model satisfactorily predicted the average growth of larval Atlantic menhaden during their oceanic phase off North Carolina. This model was fitted to larvae representing virtually the entire protracted spawning season of late October to early March. The predicted size at hatching of 3.4 mm agrees closely with laboratory observations (Powell and Phonlor 1986; Maillet and Checkley 1990). The initial rapid growth rate (0.47 mm/d during the first 20 d after hatch) probably occurs in warm (≥17°C) mid to outer continental shelf waters. As larvae are

transported nearer the coast, they enter cooler water. By the time larvae are at the midshelf front (as defined by Checkley et al. 1988), their growth has slowed. Growth continues to slow as larvae are recruited to the estuary at ages averaging 40–80 d. The upper asymptotic length of larvae (25.5 mm SL), determined from variables of the growth equation, is a reasonable approximation of the size of larvae just prior to transformation. There was probably little or no sampling bias against fish over 25 mm SL. Larvae larger than 25 mm SL have been collected at Pivers Island with the same

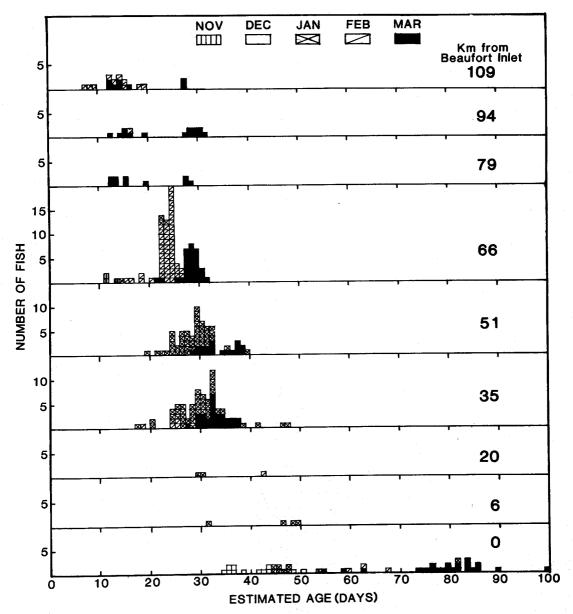


FIGURE 6.—Age-frequency distributions of Atlantic menhaden larvae collected at stations from the Gulf Stream to Beaufort Inlet, North Carolina, November 1979–March 1980.

type of gear in some years (unpublished data). In other years, such as the 1979–1980 season, larvae entered the estuary at smaller sizes and moved upstream to low-salinity zones. Lewis et al. (1972) suggested that larval Atlantic menhaden enter inlets and move upstream to low-salinity zones, where they transform into juveniles beginning at about 32 mm total length (\approx 27 mm SL).

Through their first 60 d, the average daily growth

(0.33 mm/d) of wild Atlantic menhaden larvae was about 10% greater than it was for wild gulf menhaden (0.30 mm/d; Warlen 1988). These average growth rates and different sizes at hatching contributed to the predicted sizes of 23.2 mm and 20.3 mm SL for Atlantic and gulf menhaden at 60 d. Powell (1989) showed that Atlantic menhaden produce relatively larger eggs than gulf menhaden. These eggs result in larvae that are

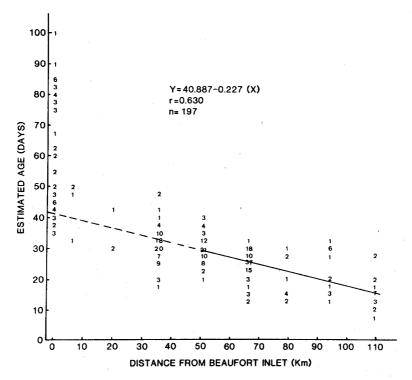


FIGURE 7.—Regression (solid line) of the estimated age (Y) versus distance from Beaufort Inlet, North Carolina (X) for 197 Atlantic menhaden larvae (numbers along solid line) collected from station 14 (51 km offshore) to station 18 (109 km offshore). Data for 134 larvae collected at stations 11–13 (6–35 km offshore) and Beaufort Inlet are plotted to show their relationship to the extrapolated (dashed) regression line.

relatively larger at first feeding and that apparently have higher rates of digestive and sensory system development (Powell 1989). These features give Atlantic menhaden a growth advantage that is reflected in their larger size at 60 d.

Atlantic menhaden eggs occur at some location along the east coast of the USA in every month except March (Judy and Lewis 1983). South of Cape Hatteras, spawning in North Carolina is confined to the period from late October to late

February. This conclusion is based on ovarian maturation (Higham and Nicholson 1964), the occurrence of eggs and small larvae (Reintjes 1969; Judy and Lewis 1983), and back-calculated birthdate frequencies of larvae collected over five spawning seasons in North Carolina (unpublished data). Spawning off North Carolina is thought to most likely occur on the mid to outer continental shelf west of the Gulf Stream boundary (Checkley et al. 1988). Although it has been suggested that

TABLE 2.—Standard lengths (SL; mean \pm SE) and estimated ages (mean \pm SE) of Atlantic menhaden larvae collected near Beaufort Inlet, North Carolina. Gear types: N = fixed neuston net (fished at Pivers Island), B = bongo nets (fished by R/V John deWolf II). The difference between the intercept (40.9 d) of the model in Figure 7 and each of the mean estimated ages of fish from five collections was subjected to a *t*-test; asterisks denote significance at $P < 0.05^*$ or $P < 0.01^{**}$.

Date	Gear type	Number of fish	Mean SL (mm)	Mean estimated age (d)	t-value (age versus 40.9 d)
Dec 7, 1979	N	12	22.4 ± 0.6	41.1 ± 1.5	0.13
Jan 23, 1980	N	9	20.7 ± 0.8	51.2 ± 4.0	2.61*
Feb 4, 1980	N	. 3	24.8 ± 0.5	63.3 ± 2.6	8.62*
Mar 19, 1980	В	23	23.9 ± 0.3	79.0 ± 2.0	18.77**
Apr 17, 1980	N	4	21.1 ± 0.7	41.5 ± 0.3	2.12

Atlantic menhaden spawn over most of the continental shelf (Nelson et al. 1977; Ahrenholz et al. 1987), the absence of young or small larvae within at least 20 km from shore seems to refute this idea for the North Carolina continental shelf.

Atlantic menhaden are able to spawn in captivity at temperatures as low as 15°C (W. F. Hettler, National Marine Fisheries Service, personal communication); however, successful early larval development is thought to occur only at temperatures of 17°C or higher (Powell and Phonlor 1986). Surface water temperatures of 17°C or higher were found during the entire spawning season in Onslow Bay off North Carolina seaward of station 15. Early in the season (November), the 17°C isotherm was closer to shore and included stations 13 and 14. Later in the spawning season, water temperatures too low (<17°C) for successful larval development may extend much farther offshore in North Carolina. Early-season (November-December) spawning may occur closer to shore (possibly within 50 km). As the season progresses, shelf waters cool (January-February), and spawning probably occurs further than 65 km from shore then.

Hoss et al. (1989) summarized several mechanisms that could be responsible for transport of larval fishes from offshore spawning sites to estuaries. Nelson et al. (1977) suggested that zonal Eckman transport facilitated surface water transport of Atlantic menhaden larvae toward shore. Miller et al. (1984) suggested a two-layered, buoyancy-driven circulation in the fall (November-December) with surface waters directed mainly shoreward and bottom water directed offshore. For winter (January-March), Miller et al. (1984) suggested a three-layered wind and buoyancy-driven circulation with thin surface and bottom layers flowing offshore and a large intermediate-depth layer flowing shoreward. Density-driven circulation of water from the outer continental shelf to the midshelf front was proposed by Checkley et al. (1988). Although their data were only for January-March, they suggested that this circulation prevails over the entire spawning and early life history period in North Carolina.

Transport of larvae from offshore spawning sites to the estuary during January–March appears to be a biphasic phenomenon. In the first phase, larvae are transported rapidly from offshore to about 20 km (January) or 35 km (February, March) outside Beaufort Inlet. These stations may coincide spatially with the midshelf front (Checkley et al. 1988), which in winter may be characterized by

narrowly separated 12-15°C sea surface isotherms. The distance of the midshelf front from shore probably varies with meteorological and oceanographic conditions, but generally moves farther offshore as coastal waters cool during winter. The second transport phase is more protracted temporally, and the overall larval transport rate to the estuary appears to be greatly reduced. During this phase, larval Atlantic menhaden must accomplish movement into the nearshore zone and then into the estuary. Prior to estuarine recruitment there may be some accumulation ("pooling") of larvae outside the inlet. This "pooling" could account at least partially for recruitment of increasingly older larvae to the estuary from January through March. Boehlert and Mundy (1988) also suggested that transport and estuarine recruitment of larvae of species spawned offshore is a two-stage process. They recognized the first as an accumulation of larvae in the nearshore zone and the second as the process of accumulation near inlets and estuary mouths and eventual passage through them.

The total transport time from spawning to estuarine recruitment (mean age of larvae collected at Beaufort Inlet) increases throughout the fall and winter, and then decreases by April. This pattern has also been observed for Atlantic croaker *Micropogonias undulatus* (Warlen 1982) and spot *Leiostomus xanthurus* (Warlen and Chester 1985; C. Flores-Coto and S. M. Warlen, unpublished data) in the same area of North Carolina. This suggests that larvae of these species spawned on the continental shelf may respond to similar mechanisms of transport and estuarine recruitment.

Behavior of larval Atlantic menhaden may play a role in their across-shelf transport rate. The larvae are most abundant in the top 10 m (Checkley et al. 1988) or 15 m (Nelson et al. 1977) of water. Hoss et al. (1989) clearly showed that Atlantic menhaden larvae 13 mm or larger require inflation of their swim bladders each night at the airwater interface. Daily vertical movements to and from the surface may place larvae in different water masses with different flow directions that could affect transport. Atlantic menhaden larvae between the coast and as far as station 17 (≈95 km offshore) are large enough to accomplish swim bladder inflation. In fall, the predominant surface waters flow towardshore (Miller et al. 1984) and larvae are transported to shore more quickly. This enhanced flow shoreward and the presumed spawning closer to shore may contribute to the recruitment of younger larvae to the estuary in fall. If the predominant surface water flow is directed offshore in winter (Miller et al. 1984) and larvae are at the surface at least part of each day, net shoreward transport rate would be reduced. The extended total transport times (i.e., ages at estuarine recruitment), particularly in February and March, support this contention. The frequency of cold fronts declines in late winter (Pietrafesa et al. 1985); the surface offshore water flow is probably reduced then, and the transport rate of larval fish from the midshelf front may increase. The observed ages of Atlantic menhaden larvae entering the estuary probably reflect changes in the transport rate as well as the distance that spawning occurs from shore. Other behavioral characteristics of Atlantic menhaden larvae that could be important to their across-shelf transport are un-

It seems likely that behavioral differences could explain why species that share a common spawning area and time are distributed differently as larvae. For instance, the eggs and early larvae of Atlantic menhaden and round herring Etrumeus teres occupy outer continental shelf waters simultaneously. Whereas most Atlantic menhaden are transported toward shore and eventually reach estuaries, round herring are virtually never found shoreward of the midshelf frontal area. During the January-March 1980 cruises, round herring and Atlantic menhaden larvae occurred together offshore of the midshelf front. However, round herring were never found closer to shore than station 14 (≈50 km offshore). This suggests that microhabitat preferences (e.g., different vertical distributions) may segregate the larvae and perhaps alter their susceptibility to passive transport (Powles 1981; Boehlert and Mundy 1988).

Acknowledgments

Thanks are due C. W. Lewis for assistance in the laboratory experiments, M. T. Boyd for preparing and reading the otoliths, and A. J. Chester and D. R. Colby for statistical advice. W. F. Hettler spawned Atlantic menhaden and furnished eggs for the laboratory experiments. D. M. Checkley, W. F. Hettler, D. S. Peters, and J. W. Smith offered valuable critical reviews of an earlier draft of the manuscript. I thank those who participated in the cruises of the R/V John deWolf II. This research was supported by a cooperative agreement between the National Marine Fisheries Service, and the U.S. Department of Energy.

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Received May 9, 1991 Accepted February 7, 1992